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Studies on the morphology of Onagraceae

I. The megagametophyte of Hartmannia tetraptera

DONALD A. JOHANSEN

(WITH A TEXT FIGURE AND PLATE II)

In his memorable paper on the embryo sac of angiosperms Guignard (1882) includes, among other species, *Oenothera tetraptera* Cavanilles [=*Hartmannia tetraptera* (Cav.) Small]. He outlines megagametogenesis in this species, and describes the mature megagametophyte as being similar in organization to the usual octonucleate type. For some unfathomable reason, this paper of Guignard's appears to have been overlooked by most of those who have worked upon the onagracean megagametophyte; at least, attention has not hitherto been directed to the fact that if a species belonging to the Onagraceae (excluding the genera *Trapa* and *Montinia*) actually possesses an octonucleate megagametophyte, this information would be decidedly interesting, if not startling, since one of the indisputable diagnostic characters of the family is the tetranucleate megagametophyte described by all other investigators since Hofmeister (1847).

Material of *Hartmannia tetraptera* being available since 1925 in my collection of the Onagraceae growing at Stanford University, it was considered desirable to re-examine this species and to confirm or disprove Guignard's observations.

Apart from the connection between this study and that of Guignard, many interesting peculiarities were observed in the ovule and associated structures and these alone were considered of sufficient interest to warrant publication.

MATERIALS AND METHODS

It will naturally be necessary to accept for granted that the species employed in this study is identical with that of Guignard, since the latter neither describes his species in any particular nor states the source of his plants. Certain historical information, however, is available. From Desfontaines (1829) we learn that as early as 1804 *Oenothera tetraptera* was cultivated in the garden of the Museum d'Histoire Naturelle in Paris and that the original source of the species is given as Mexico. *Oenothera rosea* was also cultivated, its country of origin being Peru. Curtis (1800)

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gives the native country of *Oe. tetraptera* as Mexico, adding that it was probably first introduced into England from Spain. Curtis' illustration is quite accurate, but in my plants I have never noticed the red spots on the stems and the reddish margins of the older leaves which his figure shows.

The geographical range of *Hartmannia tetraptera* is from Texas through Mexico and Central America to northern South America. It occurs also in Jamaica. It has so far been impossible to collect material from plants in their native habitat, hence recourse to cultivated plants became necessary. Live plants were secured from Mr. Carl Purdy of Ukiah, California, and seed from Heinr. Mette of Quedlinberg, Germany. In the garden only minor genetical differences were observed from 1925 to 1927, but these became more pronounced in 1928.

Purdy's plants are doubtless Texan in origin, but those grown from the German seed probably came originally from Mexico, perhaps by way of France. An examination of herbarium specimens at the New York Botanical Garden gave evidence that as one progresses northward from the Mexican plateaus into the Texan plains, the plants become larger, the foliage less dissected below, and the flowers become larger and usually take on a reddish tinge, even becoming rose-purple in color. The flowers of my plants were pure white in color, turning pinkish on dying.

H. tetraptera has been much confused with *H. speciosa* and even more so with *H. rosea.* Many of the plants circulating among gardeners as *H. rosea* are probably only rose-flowered varieties or forms of *H. tetraptera.* There is also considerable confusion regarding the plant variously known as *Oenothera mexicana rosea, Oe. rosea mexicana, Oe. Childsii* (Child's Evening Primrose) etc. This plant is identified by Bailey (1916, p. 2332) as *Oe. tetraptera* var. *Childsii.* It is distinctly a *Hartmannia* and in my garden is labelled *H. tetraptera* var. *Childsii,* it being intended that this combination shall stand until further research establishes the true status of the species. I am inclined, as is Bailey, to consider it a distinct species.

Young ovaries to illustrate the series of stages comprising megagametogenesis were trimmed down to a convenient size, placed in Petrunkewitsch's fluid, and the air removed with a special hand pump. For later stages, beginning with fertilization,

it is necessary to cut away all ovarian tissue possible. For the early stages in embryogenesis fixation in a modified formalin-acetic acid-alcohol was more satisfactory. The ovaries were sectioned both transversely and longitudinally at 12 microns, and stained with safranin, counterstained anilin blue (for permanency) or light green (somewhat fugitive on this material).

HISTORICAL RÉSUMÉ

Gates (1928) has recently given a résumé of studies on the embryo sac of the Onagraceae, hence it will merely be necessary to mention certain omissions in his summary. In addition to Guignard's paper, Gates has omitted those of Vesque (1879), Rutgers (1923) and O'Neal (1923); he fails to note that certain authors whose papers are mentioned under other headings have given attention to various details of megagametogenesis (e.g. Håkansson, 1924).

Since it is now known that nuclear behavior in most of the Fuchsias is irregular (vide Täckholm, 1915, Johansen, 1927), and in view of the notorious prevalence of parthenocarpy in the genus, it is not at all surprising that Vesque describes anomalous stages leading up to the organization of a pentanucleate megagametophyte in *Fuchsia fulgens*. His observations lose some of their quality through lack of comparison with species in related genera. Rutgers includes the Onagraceae in his study of the female gametophyte of angiosperms but makes no new morphological contribution. O'Neal describes the development of the megagametophyte and fertilization in *Oenothera rubrinervis*. The writer (Johansen, 1927) has described various stages in the development of the megagametophyte of nine Californian species.

THE OVARY AND OVULES

Although the earlier stages in the development of the ovule were not followed out in detail, there is nothing to indicate any irregularities which might later affect the organization of the megagametophyte. At the time the gametophytes are ready for fertilization, the ovary contains a large number of ovules loosely and variously arranged in each of the four locules. Some ovules are parallel to the locular wall, others are horizontally placed, while still others are reversed from the normal anatropous posi-

tion typical of the Onagraceae. Every degree of variation between the extremes is to be seen. The first meiotic mitosis occurs more or less simultaneously among all the ovules, but after that the ovules do not all develop at the same rate, consequently only a small percentage of the gametophytes are at the same stage of development or organization.

The partitions separating the locules disintegrate at an early stage, thus giving the numerous ovules more room in which to expand. The ovules, nevertheless, are among the smallest in the family and are characterized by the compactness of the various ovular structures.

Twin ovules occur frequently. They are enclosed in a common inner and outer integument and are ordinarily separated by distinct nucellar epidermal layers, though in a few instances a modified inner integument separates the two. Each twin possesses its individual hypostase. No attempt has ever been made—at least, not in this species—to ascertain the origin of these twin ovules.

This species possesses a very prominent hypostase (fig. 13), which often appears to assume the cupule form originally described by Van Tieghem (for a discussion of this subject and the pertinent literature, see Johansen, 1928). This condition is brought about when the characteristic fluid substance filling the cells comprising the hypostase permeates the inner layer of the inner integument (one layer of cells in thickness), beginning at the chalaza and extending to the apex of the ovule, where an epistase independently makes its appearance shortly after fertilization.

DEVELOPMENT AND ORGANIZATION OF THE MEGAGAMETOPHYTE

a) The megasporocyte. In *Hartmannia tetraptera* the megasporocyte does not make its appearance in the ovule at the early stage that it does in many other onagrads; the reason may possibly be found in the fact that early growth of the ovule is comparatively slow. A large hypodermal cell at the apex of the nucellus becomes larger than its fellows, shows evidence of greater metabolic activity, and is soon identifiable as the archesporial initial. It divides periclinally, the lower daughter cell becoming the megasporocyte, whilst the upper, by a succession of principally periclinal divisions, gives rise to a regular series of cell-layers be-

tween the micropyle and embryo sac (the tapetum). These divisions rapidly place the elongating megasporocyte deep in a large mass of cells, directly over the chalazal end of the ovule. There is, in this species, not the wide variation in number of layers of tapetal cells found in many other onagrads. The megasporocyte gradually increases in size, especially in length, and the nucleus moves slightly towards the micropylar end. The lower part of the cell is occasionally occupied by a vacuole, brought into existence by reason of the fact that the cytoplasm does not increase at the same rate as the cell, but it presently disappears. Preparation for the meiotic mitoses resulting in the formation of the quartet now commences. Only one megasporocyte has ever been observed in this species; it might be said in passing that I am constrained to regard with skepticism some of the published accounts of 'several archesporial cells' in various onagrads: in the earlier stages of the present work my notes read 'probably several archesporial initials,' but the fact that only a single mature megasporocyte was ever observed led to critical attention being devoted to this topic. With carefully controlled staining it was demonstrated that cells adjoining the archesporial initial may often simulate the functional appearance of the latter.

b) Meiosis. Since this paper is primarily morphological, it is not intended to enter into a detailed discussion of meiosis; this topic will be treated in a later paper in connection with a discussion of meiotic phenomena in the microsporocyte. However, it may be stated that the mode of meiosis is telosynaptic and that the normal haploid number of chromosomes is seven, the diploid fourteen (fig. 1). Variations in the number of microsporocytic chromosomes (seven, eight, ten) have been found in 1928 material; the range has not yet been determined.

c) The quartet. The reduction divisions result in the formation of four megaspores, arranged in a linear series. In so far as potentialities for germination are concerned, each megaspore is equal to the others, but the micropylar megaspore of the quartet invariably becomes functional. The three inner megaspores persist for a long time, and may even be observable after fertilization has taken place (figs. 2, 3).

d) The megagametophyte. During the growth of the functional megaspore, a gradually enlarging vacuole appears in the

chalazal portion, forcing the nucleus towards the other end of the cell (fig. 2). The size of the vacuole varies considerably, but the nucleus is always to be found near the micropylar end of the cell. When the new megagametophyte, now in the initial stages of organization, has about attained its limit of expansion, the first division occurs. The plane of the spindle of this division is always parallel to the longitudinal axis of the ovule. The binucleate condition persists for some time, during which period the sac enlarges a little more at the expense of the surrounding nucellar cells. In the second and final division, the plane of the spindle of the upper (micropylar) nucleus is transverse, while that of the lower is parallel to the longitudinal axis (fig. 3). There are two divisions only in the functional megaspore of the Onagraceae, in contrast to the three which give rise to the octonucleate gametophyte in the majority of angiosperms.

The organization of the four free nuclei into the various structures of the mature megagametophyte has not been described in detail for any onagrad, probably because the process, when once initiated, is consummated with incredible rapidity. My own observations are not as thorough as might be desirable, but they are perhaps worth recording. The two nuclei derived from the nucleus remaining in the upper portion of the sac following the second division become the synergid nuclei, while those from the lower nucleus become respectively the nucleus of the egg cell and the polar nucleus. The spindle fibers from the division of the uppermost nucleus initiate the formation of the walls surrounding the two synergids, while the lower spindle disappears immediately upon the reorganization of the daughter nuclei (fig. 4). The two walls being formed are loosely held together and are not connected by a middle lamella; this permits divergence of the walls and the assumption of the pyriform shape of the synergids. It has been very difficult to establish the exact manner in which the egg cell wall arises, if one prefers to seek a mechanical explanation rather than accept the alternative theory that it originates de novo in the cytoplasm. The only objection to this alternative is that it does not explain why a wall is not also formed around the polar nucleus. In the lower part of the diverged synergid walls an unequal split was thrice observed. This constitutes the basis for my theory that the egg cell wall, if not an outgrowth from those

enclosing the synergids, is at least stimulated into development by and during their growth. Its origin is diagrammatically explained in text-figure 1. It differs from the synergid walls in that the latter give cellulose reactions alone, while the egg cell wall has neither a pectic nor a cellulose reaction. The latter reactions were also obtained by Ishikawa (1918). Cell walls in abnormal embryo sacs are usually simple protoplasmic membranes.

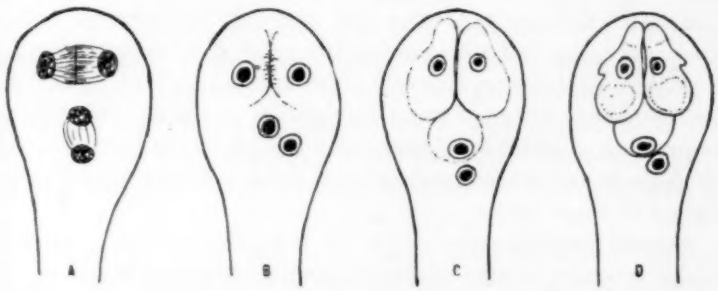

Fig. 1, *A-D*. Wall formation in the megagametophyte of the Onagraceae, based on *Hartmannia tetraptera* (diagrammatic). (A) Conclusion of the second and final division in the embryo sac. (B) Early wall formation. Notice the disappearance of the lower spindle. (C) Later stage. Wall between the synergids is definite; elsewhere it is still in a formative stage. (D) Wall formation complete; megagametophyte mature and ready for fertilization. The splits in (C) are due to the fact that no middle lamella is developed.

The egg cell is more or less open towards the apex; the nucleus together with a small amount of dense cytoplasm is crowded against the lower wall by a huge vacuole which occupies by far the greater part of the egg cell (figs. 8, 10).

The polar nucleus in about half the observed cases is non-nucleolate, a rare condition for the family. In many instances of nucleolate polar nuclei, the nucleolus has a distinctly amoeboid shape. This phenomenon has been observed in other species, and is considered a stage in the decreasing importance of the 'endosperm.' This topic is being discussed in detail in another paper of the present series.

In *H. tetraptera* the developing megagametophyte attacks the surrounding nucellar cells to a greater extent perhaps than in any other species of the family so far investigated. The female

gametophyte is always broad and densely packed with foodstuffs, hence the unusual ravages upon the nucellar cells may be explained. The starch grains are large in size but sparingly scattered throughout the entire tapetum and in the greater portion of the nucellus. However, the mass of the demolished synergids together with the remnants of the pollen tube provides the main source of nutriment during the earlier stages of embryo development.

c) The filiform apparatus and synergid indentations. This paper was ready to be forwarded for publication when the paper of Dahlgren (1928) on synergid indentations appeared. Since my conclusions are different from Dahlgren's, and a somewhat more comprehensive series of observations have been made, it was felt advisable to reconstruct and enlarge those portions of the paper relating to these topics.

Normal megagametophytes of *H. tetraptera* have been roughly divided into two classes, although the ultimate significance of the basis for the division cannot be foretold. The first class (fig 7) is characterized by the presence of the peculiar filiform apparatus in the beaks of the synergids, while in the other group (fig. 6) there is no indication whatever of this peculiarity. In other structural details the two classes are essentially similar, and they occur in approximately equal numbers in any given ovary.

Dahlgren does not devote any particular attention to the filiform apparatus, merely quoting the opinion of one writer that the formation of indentations depends upon the existence of the filiform apparatus, and quoting the converse for another writer. The median course seems preferable, since there is no indisputable evidence that a definite relationship exists between the filiform apparatus and the indentations.

The filiform apparatus, when present, is a semi-solid mass in whose lower portion are found a number of very minute canals or striations, arising in the basal part and converging towards the apex, but not reaching the tips of the synergids (fig. 7). This structure, as noted by Dahlgren, has been found in a great many plants from other families, but my observations indicate that it is especially prominent in, and characteristic of the Onagraceae. It is readily revealed by light green used in contrast to safranin, though gentian violet is more likely to indicate the delicate pores

or striations. The uppermost part of the synergid, above the striations, is a clear space, which is doubtless the repository for the chemotactic substance supposed to attract the microgametophyte. Dahlgren, however, believes that the evidence that the synergids secrete a chemotactic substance is based on 'rather loose grounds.' I do not concur in this view, for in *Clarkia elegans* I have often noticed on the external walls at the tips of the synergids large droplets of an exudate which have the identical chemical reactions of the substance contained in the apices of the synergids. Smaller droplets may even be found in the tapetum where the cells have broken apart. It appears more likely that this substance secreted by the synergids does not necessarily of itself act chemotactically towards the microgametophyte, but assists in preparing the way for the entrance of the latter by attacking the cells in the tapetum between the micropyle and the apex of the embryo sac. In those synergids lacking the filiform apparatus, the apices contain the same finely vacuolate cytoplasm as is found in other parts of the synergid outside the basal vacuole (fig. 6).

In his earlier work, Dahlgren considered the indentations to be artifacts, but later modified this view, and wrote: 'If the indentations are not attributable to methods of preparation, their origin must be dependent upon developmental-mechanical causes alone.' He believes with Asplund that they are 'certainly without any physiological significance.' To summarize my own conclusions regarding the indentations peculiar to the onagrad synergids: they are as perfectly natural characters as the filiform apparatus or the omnipresent basal vacuole, and their purpose may be both physiological and mechanical. It should be borne in mind that synergids which become haustorial, as in *Helianthus annuus* and in many other Compositae, are in an entirely different category from synergids which are prevented by comparatively thick cellulose walls from becoming haustorial. Haustorial synergids, moreover, rarely if ever possess the filiform apparatus; in such synergids, physiologically speaking, the haustorial function supplants the 'chemotactic' and to the same end.

Synergids possessing a well defined filiform apparatus apparently have a high metabolic rate, and as they become older they get more and more exhausted, since they cannot receive from

outside the equivalent of 'raw materials.' Collapse and shrinkage are inevitable unless fertilization intervenes; this is especially true of species inhabiting localities that support herbaceous plant life for two or three months only per annum. The shrinkage of synergids has no connection whatever with the presence or absence of indentations. The indentations, which extend around approximately three-fourths the circumference of the synergids, are clearly shown in text-figure 1, *D*.

The synergids have been observed to serve a definite mechanical purpose. In megagametophytes whose synergids very likely lacked indentations, the microgametophyte entered with such force that both synergids were completely demolished and the egg cell was forced beyond the center of the sac. In other species whose synergids were supplied with well formed indentations, the initial force seemed to be the same as in *H. tetraptera*, but the synergids withstood the shock without much damage to themselves. These facts furnish the basis for the writer's theory that one of the principal functions of the synergids is to serve as 'shock absorbers' against the too violent entrance of the pollen tube, thus preventing the complete demolition and consequent degeneration of the megagametophyte.

Dahlgren states that he investigated plants of the Onagraceae but found unmistakable indentations in *Clarkia pulchella* only. *Clarkia, Eucharidium* and *Godetia*, I find, are very likely to have shrunken synergids because ovaries of these genera are very difficult to fix properly. The Epilobiums have very poorly developed synergids. In other onagrads, beautifully organized synergids may easily be found in *Anogra trichocalyx, Sphaerostigma Veitchianum*, and *Zauschneria californica*.

TERATOLOGICAL MEGAGAMETOPHYTES

Many types of irregularities are frequently met with (figs. 9, 10, 11, 12), and poor organization of the megagametophyte is commonly encountered. The trouble generally lies with the primary synergid nucleus, which often fails entirely to divide; sometimes it simulates the appearance of a normal (i.e. for this species) synergid (fig. 10), and in other cases it is merely a large cell (fig. 9). In any event, it may be identified by the omnipresent basal vacuole. This recalls conditions in the markedly anomalous

megagametophytes of the garden Fuchsias. The failure of the primary synergid nucleus to divide disrupts the organization of the gametophyte; but despite the lack of normality, few supernumerary nuclei and no superfluous sacs have been observed in the hundreds of ovaries sectioned and examined.

CONCLUSIONS

In conclusion, the megagametophyte of *Hartmannia tetraptera* may be considered a pronouncedly transitory type, and this is in agreement with the idea of Broekens (1924) that the genus (=*Xylopleurum*) constitutes an intermediary group between *Kneiffia linifolia* and *Jussieua*-like ancestors. The only species of *Kneiffia* of which I have preparations available at present is *K. fruticosa* (incl. *K. linearis*), originally obtained in 1925 from Mr. Purdy's nursery. I cannot tell how closely it resembles *K. linifolia* morphologically. The synergids of *K. fruticosa,* in the majority of mature megagametophytes, possess well defined indentations, while in others this peculiarity is somewhat rudimentary. The filiform apparatus is always present.

The evidence seems conclusive that Guignard was somewhat hasty in his attempt to substantiate his thesis that the embryo sacs of all angiosperms have the same fundamental octonucleate organization. Either his observations were incomplete or his interpretations erroneous; the only explanation possible is that his two polar nuclei represent a binucleolate polar nucleus and the three 'poorly developed antipodals' are the three persistent, non-functional megaspores (consult fig. 3). The synergids and egg cell as delineated require no special criticism.

SUMMARY

1. Guignard's description of an octonucleate megagametophyte for *Hartmannia* (*Oenothera*) *tetraptera* is not confirmed: the species is as regularly tetranucleate as any other species of the Onagraceae.

2. The species is in a transitory stage, as evidenced by cytological behavior in the megaspores, megagametophytes and microsporocytes. Phylogenetic forces are in active operation.

3. The probable method of cell-wall formation in the embryo sac is described.

4. The filiform apparatus and the indentations characterizing the synergids are entirely normal structures.

5. The normal haploid number of chromosomes is 7, the diploid 14, but some variation exists.

The material was collected while the writer was a University Fellow at Stanford University; the paper was prepared during the tenure of a National Research Fellowship in the Biological Sciences, with residence at the New York Botanical Garden.

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Description of plate 11

All except figure 13, ×450. Figure 13, ×100.

Fig. 1. First meiotic mitosis in the megasporocyte. Seven haploid chromosomes.

Fig. 2. Binucleate megagametophyte. The lower three megaspores still persistent.

Fig. 3. Second mitosis in the megagametophyte. Seven haploid chromosomes on each spindle. In this instance, the three non-functional megaspores are *within* the embryo sac, the cytoplasm of one having partially united with that of the megagametophyte. It was doubtless in a case such as this that Guignard mistook the non-functional megaspores for antipodal cells.

Fig. 4. Tetranucleate megagametophyte, with the earliest observed stage in the process of synergid wall development.

Fig. 5. Organization of the megagametophyte nearly complete. The characteristic vacuole is just appearing in the synergid to the left.

Fig. 6. Mature megagametophyte representing the type characterized by the absence of the filiform apparatus.

Fig. 7. The same, but with the filiform apparatus present. In this, as in the preceding figure, the indentations are absent from the synergids. The polar nucleus in each case is non-nucleolate.

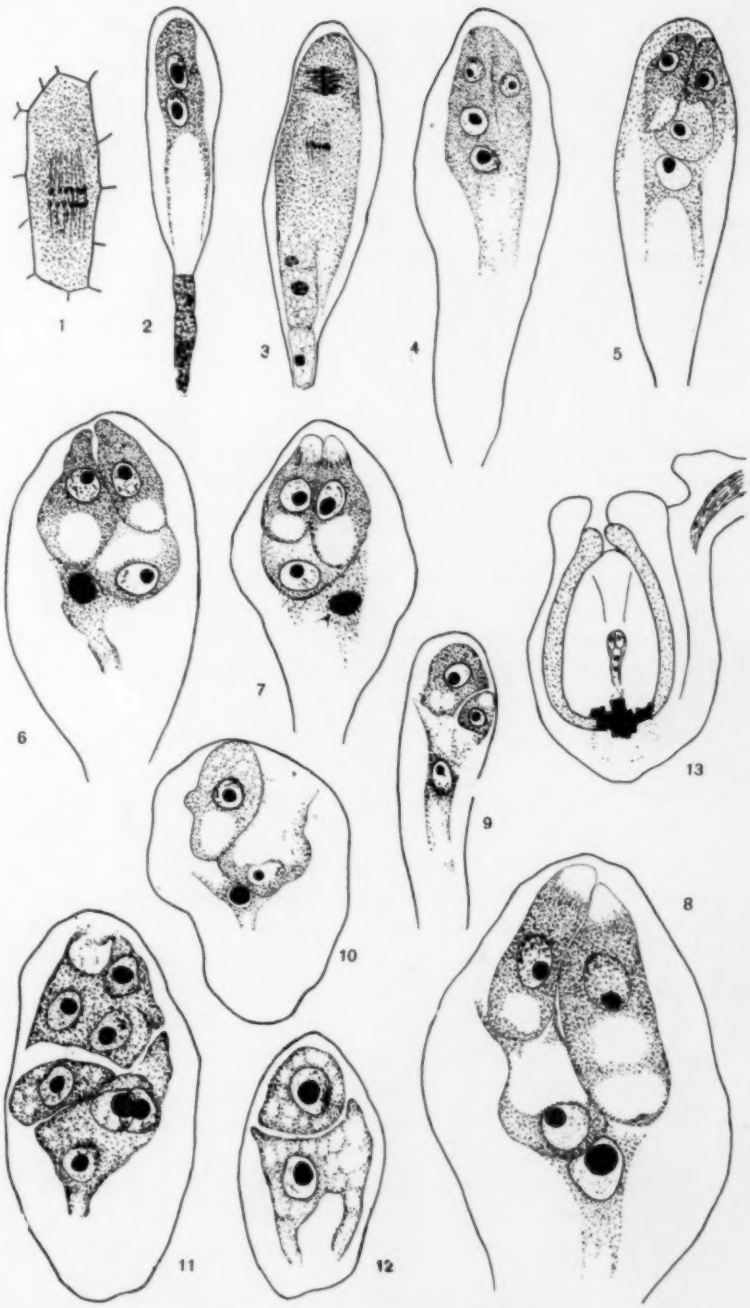
Fig. 8. Hypertrophied synergid in an unusually large embryo sac. Polar nucleus is nucleolate.

Figs. 9, 10. Abnormal megagametophytes in which the primary synergid nucleus failed to divide. The synergid in figure 10 has a double indentation.

Fig. 11. An abortive attempt to form two megagametophytes in the same embryo sac. The fourth nucleus of the upper group is in a succeeding section.

Fig. 12. Probably an earlier stage than the preceding figure. The cause seems to lie in a precocious mitosis in the functioning megaspore, with simultaneous transverse cleavage of the cytoplasm.

Fig. 13. Topography of the ovule (median longitudinal section) at the time the megagametophyte is ready for fertilization. Inner integument stippled; hypostase solid black.



JOHANSEN: HARTMANNIA TETRAPTERA

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A comparison of the behavior of crown gall and cancer transplants

MICHAEL LEVINE

(WITH PLATES 12, 13)

The transfer of small pieces of tumor tissue from one animal to another of the same species is now a well established laboratory procedure for propagating animal cancer. The view held by Jensen (1903) and confirmed by Bashford and Murray in 1904, and together with Cramer in 1905, that the growth of the transplanted portion of the tumor is responsible for the new growth in the host and is not the product of the host, is now also generally accepted (see Loeb, 1901-2).

A study of the transplanted malignant cells shows that they possess the faculty of continuous growth and utilize the tissue of the host to the fullest extent. The host tissue does not acquire the power to proliferate.

The stroma of the tumor, however, consists of a connective tissue network and a blood supply system which are the direct outgrowths of the host. The stroma forms the framework about which the rapidly dividing and growing cancer cells are formed. This reaction of the host Ehrlich (1907) attributed to specific substances formed by the tumor cells which act upon the fibroblasts and angioblasts of the host. Apolant, according to Woglom (1913) believes that the preponderance of one of these elements of the stroma over the other is due to an unequal stimulation of the *Anlagen* of these tissues. A well balanced stimulation of both elements produces a well supported and well nourished carcinoma. Gierke (1908) pointed out that the extent to which a cancerous growth develops depends upon the formation of the connective tissue and blood vessels. The character of the blood supply furnished by the host may be altered by changes in temperature. Certain hosts which are resistant to the growth of the transplant fail to produce the necessary blood supply for it.

Crown gall is a localized overgrowth of plant tissue and may be induced most readily by pricking the plant, where the plant tumor is desired, with a steel needle previously immersed in a sub-culture of *Bacterium tumefaciens*. The inoculation of this organism, preferably into the younger portions of the plant,

results in the development of an overgrowth of tissue in the region of inoculation from fifteen to thirty days later. The development of fibrovascular elements in plant overgrowths has been considered by Smith (1911) as analogous to the stroma in animal cancer.

This so-called stroma of the crown gall tissue presents a marked contrast to that in animal or human cancer. The young tumor in plants shows no fibrovascular elements. In old crown galls the fibrovascular elements, if present, may be due to the displacement of old tubes and vessels by the growth of the rapidly proliferating meristematic tissue formed about them, or they may arise, as they most frequently do, by the differentiation of the proliferating cambium tissue. In this case nourishment could hardly be brought through the disconnected and isolated vessels or tubes. These vessels or tubes arise entirely from the crown gall tissue itself and do not grow into the gall. In the former cases the crown gall tissue surrounds the old fibrovascular elements. These elements are not capable of further growth once they are fully developed.

The transplantation of crown gall tissue to healthy parts of the same plant (autotransplant) or to other plants (homeo- or heterotransplants) has never been a question of the propagation of this disease. The transplantability of crown gall tissue to healthy plants is another means of comparing the proliferating power of crown gall and cancer cells, and of establishing any analogy that may exist between them.

Jensen (1910, 1918) compared the neoplasms of animals and plants, and raised the question of the transmissibility of this plant disease by transplants. He transplanted inocula of crown gall tissue of spontaneous and artificially produced origins to healthy plants of the same species. Jensen (1918) figures the results of successful transplantations of crown gall tissue from the yellow sugar beet to the red mangel, and of the crown gall tissue of the latter to healthy roots of the former. He contends that the tumors formed are due exclusively to the growth of the transplanted crown gall tissue, which corresponds in appearance and structure entirely to the mother tumor. It is of importance to note that isolation of *B. tumefaciens* from the spontaneous crown galls of mangels and sugar beets was suc-

cessful in only one case. Jensen believes that while *B. tumefaciens* causes crown gall in beets, the bacteria die off in older plant overgrowths. He was unable to recover this organism from crown galls produced by transplanted tissue of spontaneous origin. Jensen thinks it extremely probable that the cells of the tissue under the influence of the bacteria become altered for a series of generations and develop the increased proliferating power which becomes independent of continued stimulation. Jensen states that tumors on beets produced artificially through the agency of *B. tumefaciens* behave like spontaneous growths. Jensen obtained the same results with his transplants whether he used spontaneous or artificially produced tumors. On the basis of these observations Jensen holds to the opinion that crown gall is analogous to animal cancer.

In view of these results it has seemed to me to be of interest to study further the transplantability of artificially produced crown galls and their effects on the host of similar species. Another point of interest is to test the effect of crown gall tissue of one species of plant transplanted on widely separated species. The production of crown gall disease under these conditions would tend to indicate that this is an effect of the bacterical organism present in the transplant rather than the growth of the inoculum. Spontaneous crown galls, according to Jensen, have few or no bacteria, while artificially produced crown galls in my studies yield an abundance of *B. tumefaciens* under proper cultural conditions. It has been shown (Levine, 1923) that the number of bacteria introduced into a wound in the plant is of no importance in the production of the overgrowth.

It is with crown gall of the artificially produced type that my tests were made in order to throw further light on the question of the behavior of crown gall transplants and their analogy to transplants of animal cancer.

MATERIAL AND METHODS

Experiments on the transplantability of crown gall tissue to healthy plants were started in the spring of 1925 and were carried on for three consecutive summers. Most of the tests were repeated two and three times. The plants studied were

grown in the garden. A large number of the experiments were carried over the winter season in the greenhouse and in a well lighted room. The garden space was divided into a number of plots, each of which was sown with seeds or cuttings of one species of plant. The castor bean *(Ricinus communis)*, tomato *(Lycopersicum esculentum)* var. earliana, and the beet *(Beta vulgaris)* vars. garden beet, yellow tankard, and red colossal were the chief sources of crown gall tissue as well as hosts for the transplants. The geranium, tobacco *(Nicotiana affinis* and *N. Tabacum)*, the rubber tree *(Ficus elastica)* and the rose plant were used primarily as hosts.

Some of the plants in each plot were inoculated with young or old sub-cultures of a virulent strain of *B. tumefaciens*. Only young petioles and growing points of the plant were used for study. Crown galls were formed in all plants by the inoculation of the bacterium fifteen or thirty days later. *N. affinis* in my cultures failed to yield crown galls on inoculation with this organism. These plants remained immune to crown gall throughout this experiment. In 1928 over 200 inoculations were made with *B. tumefaciens* in over 100 plants of this species without producing any overgrowth.

Young crown galls used for inoculation purposes were removed together with a larger portion of the plant on which they were growing. The shoot, root, or leaf was taken to the laboratory, where the crown gall was removed with a sterile knife and forceps. The gall was washed several times in sterile water and was then subjected to a weak solution of bichloride of mercury for several minutes. The entire gall was again washed in sterile distilled water. The crown gall was then cut into wedge-shaped fragments, the greatest measurement of which was about 1 mm. to 3 mm. These were placed in a sterile Petri dish and were then introduced into the tissue of the healthy plants. A small wedge-shaped incision was made in the host plant and the inoculum was introduced so that the outer surface lay inside of the surface of the host. An inoculum larger than the size of the incision was selected so that gentle pressure was required to make the host tissue hold the inoculum in place. In a few cases two or three turns of a lightweight cheese cloth were placed about the host over the region

of the inoculation. In the case of the beet transplants, the root was uncovered for a short distance below the crown and the inoculum was introduced into the incision made there. There appeared to be no marked difference in the result obtained whether the upper part of the root was covered again with soil or remained exposed. The covered roots were subject more often to worm infections.

Crown gall tissue of the castor bean was transplanted to the same plant (autotransplant), to other castor bean plants (homeotransplant), and to other plants of different genera such as the tomato, geranium, rubber plant, and garden beet (heterotransplant). Crown galls of the tomato were studied in the same way. The crown gall of the yellow tankard mangel was transplanted to the red colossal mangel and the common garden beet. The crown gall of the latter was transferred to the roots of the first. Crown gall tissue of the beet induced by *B. tumefaciens* inoculations was also tested on the castor bean, tobacco, and tomato plants.

Control studies were made on the same plants that received crown gall inocula. The control tissue used consisted of small fragments of young petioles or growing points free from crown gall tissue or *B. tumefaciens*. All the plants were carefully labeled at the region where the inoculation of the tissue was made. Crown galls produced by crown gall transplants were used again for inoculating purposes in a manner similar to that described above.

Microscopical examinations of the hosts with their transplants were made. Cultural studies were made of the organisms isolated from the crown galls used as transplants and from those derived from the transplants.

BEET CROWN GALL

Transplantable animal tumors once established may be propagated from animal to animal with considerable ease for many generations. In this case it is generally accepted that the transplanted tissue is alone responsible for the new growth. A framework of connective tissue and a blood supply is developed by the host for the new growth. The results given in this report are derived from a study of the effects of crown gall in-

ocula on the host after auto-, homeo-, and heterotransplants were made in order to determine the analogy of this plant disease to cancer in animals and man.

The chief subjects of this study were the castor bean, the common garden beet, the yellow tankard mangel, and the tomato. The tobacco, geranium, the rubber plant, and the rose plant were used as hosts. Artificial crown galls were produced by inoculating growing parts of these plants with a culture of *B. tumefaciens.*

It may be of interest to note that the color of the pigment in the crown gall of the garden beet resulting from the bacterial inoculation is a deep maroon color at the margin while the inner portions contain a yellowish-red pigment (fig. 18). The crown gall of the red colossal mangel (fig. 17) lacks pigment in the interior, while the surface is reddish in color, resembling that of a small spring radish. The crown gall on the yellow mangel presents similar variations in color. The yellow pigment is distributed over the surface of the gall and is identical in shade with the color of the normal roots. The interior of the gall is streaked with a faint yellow pigment or may be entirely lacking in pigment. It must be borne in mind that there is no sharp demarkation between the pigmented and non-pigmented areas. There is a tendency of one colored zone to blend with the other. Recognition of these color differences aids one in tracing the growth of the inoculum.

As mentioned above, pieces of crown gall tissue on the common garden beet produced artificially by the inoculation of the root with a virulent strain of *B. tumefaciens* were transplanted to eighty young roots of the yellow mangel. The greater number of these inocula failed to grow or take hold of the host or produce any overgrowth. These roots (48 in number) after three months showed normal scar tissue without evidence of crown gall formation.

In thirteen cases crown galls of the host appeared thirty days after the transplant was made. These were typical crown galls of the yellow mangel with a dense yellow pigment on the surface and pale yellow or non-pigmented tissue in the interior. In these cases the red colored inoculum from the garden beet

crown gall had disappeared or could be seen as a small shriveled and blackened body lying in the scar of the root.

In three cases undeniable growth of the transplanted garden beet crown gall occurred. The inoculum had become attached to the host tissue and developed into a gall of appreciable size as shown in figure 19. This photograph represents the root of a young yellow mangel upon which a typical garden beet crown gall has formed, cut longitudinally through the gall and the root. Here, however, one finds evidence supported by observations given below on a large number of heterotransplants that the host tissue is also involved in the formation of the growth of this tumor. Freehand sections of these roots enabled me to trace the growth of the host and the inoculum. The photograph shows clearly that the crown gall arises from the lower surface of the incision made in the host. The upper surface of the incision now appears as a dark narrow compressed band of tissue which shows no evidence of growth. The lower surface of the cut in the host has proliferated and formed part of the crown gall. Bands of faintly yellow colored tissue may be traced from the surface of the host into the grown inoculum. A microscopic examination of the tissues at above and below the region where the transplanted crown gall and host meet, as shown in figure 20, leaves no doubt as to the stimulation of the host to crown gall formation. The yellow pigmented tissue found in the crown gall of the garden beet is not to be confused with the color of the yellow mangel crown gall. While I made no analysis of these two pigments, the color differences are so striking that the one cannot be confused with the other. The major part of the crown gall in this case is shown in the photograph (fig. 19) as a deep red globular mass of tissue, while fainter red and yellow portions may be seen at the region of union of the host and transplant as indicated by the arrow. The shade of the yellow pigmented areas is typical of the color of the crown gall on the yellow mangel produced by an inoculation with *B. tumefaciens.* The passage of yellow pigment from the host into the crown gall inoculum is questionable. Hoffmann (1927) in studying reciprocal grafts of pigmented and non-pigmented bean plants finds no evidence for the movement of pigment from host to graft or the reciprocal.

Sixty roots of the garden beet and the colossal red mangel were inoculated with pieces of crown gall produced by the inoculation of *B. tumefaciens.* One root was observed in which the inoculum succeeded in establishing itself. The yellow colored gall was easily recognized. Sections of this gall showed clearly the presence of red tissue of host as evidence of its proliferation. Necrosis followed rapidly the removal of this plant from the soil so that photographic reproductions were made impossible. In eight cases in this series typical red crown galls developed after inoculating the garden beet and red mangel with crown gall tissue of the yellow tankard. The inocula in most of these roots were still to be identified although they had degenerated into very small particles of matter held firmly by the partly enveloping scar tissue. The remaining roots in this experiment showed only scars of varying size without any evidence of proliferation equal to crown gall formation.

While the number of cases cited here of successful transplants of inocula are few, the evidence is quite clear that crown galls may be produced on healthy plants by introducing pieces of crown gall tissue irrespective of the success of the transplant in establishing itself. When the transplanted crown gall tissue succeeds in establishing itself on the host, the transplant as well as the host takes part in the formation of the new crown gall. It appears that the crown gall transplant behaves like an ordinary graft for a limited time, yet, due to its inherent pathogenic properties, it is capable of further growth and also of stimulating the host to proliferation. Control studies made with sterile tissue gave scars only. The newly formed tissue of the host in successful crown gall transplants is not analogous to the stroma of the animal tumors (Levine, 1925). The fibrovascular elements found in crown gall tissue arise from the development, differentiation and aging of crown gall cells.

Heterotransplants were made in which the crown gall of the beet was inoculated into young nodes and petioles of castor bean plants. These inoculations were carefully made so as to avoid undue injury in order to secure the best advantages to the implanted tissue. The inocula were carefully watched from day to day. Light bandages were applied in a number of cases to prevent drying out of the inocula. In twenty cases studied it

was observed that the inocula grew smaller and finally dried up in spite of the protection of the cloth. However three plants in this series of experiments produced crown galls of the globular type at the bases of the scars formed. Figure 5 is a photograph of a *Ricinus* stem inoculated with a piece of garden beet crown gall. The crown gall in this picture represents the overgrowth of the host entirely, since the beet inoculum has long disappeared. Figure 6 represents a longitudinal section of the same stem. The area below the gall, indicated by the arrow, shows the region occupied by the transplant in which considerable necrosis of the tissue is to be seen.

Thirty tobacco plants *(N. affinis)* which failed to respond to inoculations with *B. tumefaciens* yielded one small questionable crown gall. The dead inocula were found in the scars of the host.

CASTOR BEAN CROWN GALL

Crown galls on the castor bean *(Ricinus communis)* produced by a culture of *B. tumefaciens* were used as transplant material. Sixty-two homeotransplants were made which yielded forty-four crown galls on as many plants. In no case was there any evidence of the proliferation of the inoculum. The transplanted inocula were so inserted into the tissue of the host that they were exposed to view, yet they were not unduly exposed to the direct light and heat of the sun. The inocula were observed to dry up in all cases in this series. A large scar was formed, due to the subsequent growth and elongation of the tissue inoculated. This was followed by the development of one or more crown galls (fig. 1) in each scar twenty to thirty days later. Twenty-five control inoculations made on petioles and stems of the same plant with healthy bits of tissue produced only callus tissue without crown gall formation (fig. 2).

A small number of autotransplants of crown gall tissue was made on the castor bean. In each case a crown gall was formed on the host without the growth of the inoculum. Second and third generation homeotransplants were made from crown galls produced by inoculating crown gall tissue. Figures 3 and 4 represent the growths obtained in these experiments. The number of tests made indicates clearly that crown gall tissue formation may be induced in this manner. The galls formed, how-

ever, are due entirely to the proliferation of the host rather than the inoculum. The percentage of galls formed from second and third generation crown galls is small. This may be accounted for by the lateness of the season, when the growth of the plant usually becomes retarded. This is consistent with the reports that crown gall formation depends in a large measure upon the capacity for growth of the inoculated tissue. Nine homeotransplant crown galls were produced from inocula of first generation crown galls in twenty-one inoculations, while only two crown galls were produced when the latter galls were used as inoculating material. Autotransplants of second generation crown galls produced six galls in as many inoculations and plants.

Ricinus crown galls produced by *B. tumefaciens* were further studied by transplanting pieces of this tissue to thiry-four young shoots of the tobacco plants, *N. Tabacum*. Crown galls were produced on five plants. One of these crown galls produced typical tobacco leaves. There was no evidence of the growth of the inocula.

TOMATO CROWN GALL

The behavior of tomato crown gall transplants was also studied in a similar manner. Crown galls on the tomato plant produced by *B. tumefaciens* of different cultural ages were used. In one case eleven homeotransplants were made, in the other case twenty-one homeotransplants were made. In all cases crown galls were observed on the hosts in thirty days. Figure 7 represents the stem of a pot-grown tomato plant inoculated with a small piece (2-3 mm.) of crown gall tissue produced by inoculation with *B. tumefaciens*. A longitudinal section through this stem seems to bear evidence for the limited growth of the inoculum. The margins of the stem of the host where the incision was made show excessive proliferation, indicating crown gall formation. In figure 8, a more vigorous garden-grown tomato stem is shown that had been inoculated with tomato crown gall tissue. The inoculum was introduced into a perforation made in the stem. Two masses of crown gall tissue appear on both sides of the stem. Figure 9 represents a similarly treated tomato stem. Here the inoculum may be seen held between the two masses of crown gall tissue, but is not a part of the new

crown gall. A longitudinal view of a similarly inoculated stem shown in figures 8 and 9 is represented in figure 10. The necrotized inoculum may be seen in the pith in the lower section of the stem.

In these experiments a number of the transplants appear to be completely surrounded by the crown gall tissue formed by the host so that I found it difficult to determine whether or not the inoculum succeeded in establishing itself in the host. In the majority of cases a series of longitudinal sections through such stems showed the inoculum as a completely necrotized tissue in the center of the host-formed gall. In several cases, slight growth of the inoculum occurred. Microscopic examination of these galls showed, however, that the major portion of the crown gall was due to the overgrowth of the host.

Heterotransplants were made in which crown gall tissue of the tomato was introduced into growing portions of twenty-one tobacco plants *(N. Tabacum)*. While a large number of these inoculated plants failed to show any reaction other than a callus, seven plants produced well developed crown galls, three of which differentiated and formed typical leafy shoots of the tobacco. Figure 13*a* is a photograph of a tobacco stem with an inoculum of the tomato still visible. The wound has healed and the inoculum is dead. No crown gall is expected. In figure 13*b* two small crown galls are seen. These have been produced by a similar inoculum from the same tomato crown gall. The inoculum was introduced into the tobacco stem forty days earlier. In figures 14 and 16 well developed leafy crown galls may be seen. These arose after an inoculation with an inoculum from a tomato crown gall. In figure 16 a portion of the stem was removed to show the crown gall and its leaves more clearly. Figures 15*a* and 15*b* show entire and longitudinal section views of a tobacco stem similarly treated as above. The host tissue alone takes part in the formation of the crown gall. The inoculum is imbedded in the pith of the stem and is apparently dead.

Similar heterotransplants were made with the crown gall of the geranium and the tomato plant as the host. Figures 11 and 12 represent two views of a tomato plant inoculated with crown gall tissue of the geranium. Here also it is seen that while the host forms the crown gall the inoculum dies and

plays no further part in the development of the crown gall. The arrow in figure 11 indicates the position of the dead inoculum. The crown gall appears below it in the form of a small globular mass of tissue which on microscopic examination shows small parenchymatous cells.

Homeotransplants of geranium give similar results to those already described for the beet, *Ricinus*, and tomato. Plants such as the dahlia and potato, which failed to produce crown galls on inoculation with *B. tumefaciens*, failed to respond to inoculations with crown tissues of the geranium or tomato. A large number of inoculations were made.

In the above listed experiments, similar portions of the gall used for inoculation purposes were plated and in all cases *B. tumefaciens* was recovered, as determined by inoculations into healthy plants.

SUMMARY AND CONCLUSIONS

1. Auto-, homeo-, and heterotransplants of crown gall tissue are capable of exciting crown gall formation in the host when the host is capable of responding to inoculations of *B. tumefaciens*.

2. Crown gall tissue of the common garden beet may be grafted on the yellow mangel.

3. The graft or inoculum successful in establishing itself on the host is capable of further limited growth, but then it also stimulates the host to crown gall formation.

4. Crown gall transplants differ from the transplants of animal tumors in that the crown gall transplant does not form the sole substance of the new overgrowth. The stroma of the animal tumor has no analogy in the crown gall tissue. The fibrovascular elements found in the crown gall result from the differentiation of the parenchymatous tissue that makes up the crown gall.

5. Crown gall of the host after the introduction of an inoculum of crown gall tissue is not due to the growth of the inoculum, but results from the changes which succeed the introduction of *B. tumefaciens* with the inoculum. Plated cultures of parts of the crown gall tissue from which inocula were taken always yielded in my experiments an abundance of *B. tumefaciens* as

determined by culture studies, stained smears, and subsequent inoculations.

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Description of plates 12, 13

Plate 12

Fig. 1. *Ricinus* petiole inoculation with a single inoculum of crown gall tissue from the petiole of another *Ricinus* plant.

Fig. 2. Control inoculation made with an inoculum of normal tissue.

Figs. 3, 4. *Ricinus* petiole with crown gall of the second and third generations induced by crown gall inocula from the *Ricinus*.

Fig. 5. Crown gall on the *Ricinus* stem produced by inoculating a small piece of crown gall from sugar beet.

Fig. 6. A longitudinal section of the same stem. The necrotic area below the gall, indicated by the arrow, shows the region of the transplant.

Fig. 7. Tomato stem (grown in pot) inoculated with portion of crown gall developed on the same plant.

Fig. 8. Tomato stem (grown in field) inoculated with portion of crown gall from another tomato plant. Crown galls appear on both sides of the stem.

Fig. 9. A similar experiment in which the inoculum is still visible as a necrotized body between the two globular masses of crown gall tissue.

Fig. 10. A longitudinal section of a tomato stem showing necrotized pith of the host with small overgrowth arising from the cortex and epidermis.

Figs. 11, 12. Two views of a tomato stem (grown in pot) inoculated with crown gall of the geranium showing crown gall formation of the host.

Fig. 13 *a*. Tobacco stem with tomato crown gall inoculum. 13 *b*. Tobacco plant showing formation of small crown galls after inoculation with tomato crown gall.

Fig. 14. Tobacco stem showing the development of a leafy crown gall after inoculation with tomato crown gall.

LEVINE: CROWN GALL TRANSPLANTS

Plate 13

Fig. 15 *a*. Longitudinal section of tobacco plant inoculated with tomato crown gall, showing considerable callus tissue and a small crown gall. 15 *b*. A longitudinal section of a tobacco stem similarly treated showing the development of embryonic tobacco leaves arising from a small globular crown gall.

Fig. 16. A section of tobacco stem similar to one shown in figure 14. The stem was cut so as to expose the globular crown gall from which a leafy shoot has arisen. The stem was inoculated with a piece of tomato crown gall tissue. The removed portion of the stem is shown to the right in the figure.

Figs. 17, 18. Colossal long red mangel and a garden beet respectively, with crown gall, resulting from an inoculation with a virulent strain of *B. tumefaciens*. Both figures indicate the absence of pigment in the center of the crown galls, or show only a small diffused quantity of pigment as compared with the surface of the gall and normal root.

Fig. 19. Yellow tankard mangel, showing growth of a transplanted garden beet crown gall tissue. The arrow indicates the presence of yellow pigmented tissue of the yellow mangel.

Fig. 20. Microscopical section of the root of the yellow mangel in the region of the union of the host and crown gall tissue of the garden beet, showing an excessive proliferation of the host and the transplant (photograph made with the aid of obj. 32mm., oc. K 20, bellows 55 cm., filter K 2, W.W. panchromatic plate).

16

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18

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a 15 b

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UNIV. OF MICH.

Notes on Arundinaria

CLAIR A. BROWN

The manuals on the flora of the eastern and southern United States include two species of 'cane' or native bamboo, namely, *Arundinaria macrosperma* Michx. and *Arundinaria tecta* (Walt.) Muhl., both of which are supposed to flower at irregular intervals.

Characteristics usually used for separating these two species are as follows: *A. tecta* has canes less than ten feet tall with flowers developing in terminal panicles on radical shoots, while *A. macrosperma* has canes more than ten feet tall, with flowers developing in lateral panicles on the old canes.

From time to time questions have been raised in regard to the identity of these species. In their discussion of them, Scribner and Merrill[1] state that:

> *A. tecta* has been treated by some authors as a variety of *A. gigantea (A. macrosperma)*. Although possibly not specifically distinct, the two are found growing together under like conditions, and under these circumstances the one is readily distinguished from the other. Rarely found in bloom.

Recently, Harper[2] has made the following statement:

> This genus *(Arundinaria)* is not fully understood, partly on account of the scarcity of flowers and seed, and the number of species in North America may be anywhere from one to three or four. In Alabama there seems to be two possibly three.

He gave a description of these forms including three illustrations.

In regard to the irregular flowering of one of the species of *Arundinaria* Cocks[3] wrote as follows:

> In view of the fact that it is so often stated that this plant [*A. tecta*] blooms only at intervals of several or many years, it is worth noticing that certain clumps have been observed by the writer near Abita Springs, which have bloomed every year in the latter part of May, since 1899.

[1] SCRIBNER AND MERRILL. Grasses of Tennessee p. 128. 1894.

[2] HARPER, R. M. Monograph of the economic botany of Alabama p. 72-77. 1928.

[3] Cocks, R. S. Annotated catalogue of grasses growing without cultivation in Louisiana. Gulf Biologic Station Bull. 10: 40. 1908.

On account of the difficulty of determining with any degree of satisfaction specimens of *Arundinaria* collected in South Louisiana, a study has been made of the genus. Spikelets of *Arundinaria* were first collected by the writer in March, 1927, in a canebrake near Baton Rouge, Louisiana (*no. 989*). These were from the lower nodes of old canes that had been cut off one or two joints above the ground.

In November, 1927, a considerable portion of the canebrake in which the above specimens were collected was cleared. During the last of March and April, 1928, flowers were again found on the lower nodes of the cane stubble. For the purpose of comparison a specimen of *A. macrosperma* was then obtained from Professor A. S. Hitchcock. In the letter accompanying the specimen, Professor Hitchcock wrote: 'I have not been able to separate *A. macrosperma* and *A. tecta* in an entirely satisfactory manner. . . . . I am sending you a specimen I take to be *A. macrosperma.*' When the specimen was examined it appeared to be identical with the Louisiana specimens which had been recently collected and which had been called *A. tecta.*

About the first of May there appeared in the same field a large number of somewhat shrubby radical shoots which bore terminal panicles, and according to the manuals should be *A. tecta.* An examination was then made of the canebrakes near Baton Rouge, Louisiana, and in several places flowering specimens typical of *A. macrosperma* were found. As it appeared that flowers of the two species had been collected, material of each was sent to the Grass Herbarium in Washington. The radical shoot form *(no. 2112)* was identified as *A. tecta,*[4] and the form with flowers on the old canes *(no. 2125)* as *A. macrosperma.*

In one of the places where the cane was found in bloom a drainage ditch had been dug in the early part of January, 1928. In this place, flowers were found both on radical shoots and on the old canes. On digging up some of the plants, it was found that some radical shoots with flowers *(A. tecta)* came from the same rootstock as did stalks with lateral spikelets *(A. macrosperma).*

[4] Identical with figure 1, in The Genera of Grasses of the United States, by A. S. Hitchhock.

With the idea that flowers of *Arundinaria* could be produced by cutting off the old canes at certain seasons, or by reducing the water supply as was done by the drainage ditch, several canes were cut in November, 1928, in the place where *A. macrosperma (no. 2125)* was collected. In the spring of 1929, the place was visited again and it was found that the canes which had been cut off from one to three joints above the ground had flowered from the lower nodes.

A careful examination of several other canebrakes in flower during the spring of 1929 has resulted in finding flowering radical shoots attached to the same rootstock as the old flowering canes. One collection *(no. 2435)* was made near Erwinville, Louisiana, on the edge of a thicket which had not been cut or drained for several years. This suggested that both forms of *Arundinaria* may occur on the same rootstock naturally and that cutting or some other stimulation may not be necessary.

Another point mentioned in the literature is that the old canes of *A. macrosperma* die after they fruit. This differs from the recent observations. Canes that were known to flower in 1928 were cut in the fall and next to them were left some that were not cut. Both remained alive, and in April, 1929 the stubble of the cut canes flowered from the lower nodes, as has been stated.

One might inquire as to the reason for the difference in size between the small woody canes the size of a lead pencil and only a few feet tall and the large woody canes one to one and a half inches in diameter and up to thirty feet tall. It has been noticed that there are many patches of this small type. The only explanation that can be offered is that there must be some difference in soil or moisture conditions which hinders the growth of these plants.

Since it seems certain that the different forms of *Arundinaria* which in the past have been considered two distinct species are in reality but one, it becomes necessary to decide which name is valid. Professor A. S. Hitchcock has kindly written the following opinion concerning the valid name: 'In 1788 Walter published two species of *Arundo,* the first *Arundo gigantea,* the second *Arundo tecta. Arundo tecta* was transferred to *Arundinaria* by Muhlenberg in 1817. *Arundinaria gigantea* was described by Chapman in 1860, but there is no evidence that this was based upon

Arundo gigantea of Walter. Under the rules of nomenclature it would be necessary to consider this as an independent description, consequently *Arundo gigantea* Walter cannot be transferred to *Arundinaria* because of the presence of *Arundinaria gigantea* Chapm. Although the names are the same and the species probably identical they must be looked upon as independent names. Consequently *Arundinaria gigantea* cannot be taken up. The valid name for the large cane then becomes *Arundinaria macrosperma* Michx., 1803. Since *Arundo tecta* is the older name, dating from 1788, it would seem necessary to take up this if the two forms are considered as one species.'

It would seem then, that the name *Arundinaria tecta* (Walt.) Muhl. should be used for the common southern cane or bamboo, and that the description should be changed so as to include the characters which have been previously used for both *A. tecta* and *A. macrosperma*.

The writer wishes to acknowledge his indebtedness to Professor A. S. Hitchcock for his identifications and opinion on the valid name; and to Dr. C. W. Edgerton for his helpful criticisms.

DEPARTMENT OF BOTANY
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Development of the pollen grain and the embyro sac of Agropyron repens

MAY MOWERY

(WITH PLATES 14, 15)

Agropyron repens L., known under several different popular names, but commonly as quack grass, is a close relative of wheat. Its history as an Old World pest as far back as there is definite record, its characteristics and habits, methods of control, etc. have been treated by Kephart (1923), who regards it as the most notorious of all weeds, with the possible exception of the Canada thistle.

Material for this morphological study was collected and fixed during the summers of 1925 and 1926. Two methods of dissection were used: first, removing the lemma, and fixing the palea, with the enclosed flower, second, removing both lemma and palea and fixing only the essential organs. The first method proved most satisfactory, especially for younger stages. For fixation, Flemming's weaker solution and Allen's modification of Bouin's both gave good results. The material was imbedded in paraffin, cut at eight to twelve microns, and stained in iron haematoxylin.

MICROSPOROGENESIS

The microsporangium is derived from the outer layer of the periblem, as is usual in angiosperms. There are three stamens in each floret. The development of the anther is typical, and like that of the wheat as described by Percival (1921) in *The Wheat Plant*. The anthers develop in spring, growing rapidly just before anthesis, as becomes evident from the stages found in a young spike in June: longitudinal sections of a spikelet similar to that outlined in Percival's figure 92 (page 115) then show three florets in which sporogenous tissue has differentiated, and two primordial flowers: the fifth floret does not develop. In the climate of southern Minnesota anthesis occurs from the middle to the last of June. At first a homogenous mass of meristematic cells covered by an epidermis becomes four-lobed at an early stage. The sporogenous tissue developing from the outer layer of the periblem appears at the time the lobes become evident. The divisions previous to the formation of the spore-mother-cell

occur rapidly. The radially elongated cells divide equally and almost simultaneously, by periclinal walls, forming a primary parietal layer which forms the wall of the anther, and a primary sporogenous layer. The primary parietal layer divides to form the endothecium, a middle layer, and the tapetum. The formation of the tapetum, coincident with the spore-mother-cell stage, reaches its maximum at the tetrad stage of the spore-mother-cell, at which time it is a prominent layer of two-nucleate cells. After the sporogenous tissue has divided to form the spore-mother-cells, they grow larger and round up somewhat. Then follows the heterotypic division.

The nuclei of both the vegetative cells and the cells of the sporogenous tissue are characterized in *Agropyron repens* by several distinct nucleoli. The nucleus of the microspore-mother-cell shows a network upon which are distributed chromatin granules, and one distinct globular nucleolus. The chromatin granules take a definite stain. The cytoplasm of the spore-mother-cells does not appear to be as dense as that of the tapetal cells, which are easily distinguishable by their heavier stain. It appears to be a fine network with small granules, which does not take the stain readily. In figure 1, the nuclear net is quite pronounced, its strands having become noticeably thick. Figure 2 represents a stage of synizesis in which the nucleolus, although centrally located, is discernible. In figure 3 the granules are distinctly massed and appear to be made of larger lumps, with a large nucleolus lying just outside the mass, which shows clearly the forming spireme. In figure 4 there is evidence of a longitudinal split in the thickened spireme, as well as indications of breaking up into chromosomes. As the thread breaks up into rod-like chromosomes the nuclear membrane disappears, but the nucleolus still persists. The spindle appears as a number of fibers which attach themselves to the chromosomes and converge at the poles. Figure 5 shows late anaphase, the rod-like chromosomes being very prominent as they approach the poles.

During the heterotypic division, usually only one stage is represented in an anther at any one time. In the homotypic division, this is not the case; for two or three stages of mitosis are represented in one longtiudinal section. The chromosomes at the time of anaphase (figs. 7, 8) appear as slender bodies often somewhat U-shaped, two of them remaining away from the gen-

eral mass. The count made from this stage, using Belling's method, was twenty-one. The formation of the cell walls is successive (figs. 6–9). The four granddaughter nuclei (fig. 9) are alike in size, amount of chromatin, and in having several nucleoli. These grow to twice their first diameter (fig. 10) but in other respects appear much the same. The cytoplasm in these cells as well as in the tetrads has a distinctly radial tendency.

After the two divisions the young microspores become invested by a wall independent of the wall of the mother cell. This soon becomes differentiated into two layers, the intine of cellulose and the outer cutinized exine.

The first new feature in the development of the microgametophyte is the appearance of the germinal aperture, a thin spot in the exine, which can be discerned before the nucleus enlarges prior to division. This single aperture is characteristic of pollen of Gramineae (figured by Percival, 1921, for *Triticum*). When the nucleus divides, it forms the tube nucleus which is characterized by a single nucleolus, and the generative nucleus, which divides immediately to form the sperm nuclei, which at first appear small (fig. 11), but inclosing large nucleoli. The wall now becomes thicker and somewhat sculptured, and the sperm nuclei lengthen out. Figure 12 shows the appearance of the male gametophyte at the time the pollen is shed.

MEGASPOROGENESIS

The megasporangium originates as does the microsporangium on the outermost layer of the periblem. At first the epidermis of the member upon which the ovule is to appear is even. Cell division in the epidermis at first radial but in different directions in the hypodermal layer causes a slight protuberance. This becomes more and more evident and constitutes the nucellus of the forming ovule (fig. 13). Soon one of the hypodermal cells becomes slightly enlarged and takes a deeper stain, indicating its sporogenous nature (fig. 14). This cell enlarges so that by the time it begins to divide it is about four times the size it was when it first began to differentiate from the other cells. About this time a slight protuberance at the base of the nucellus indicates the first integument. The beginning of the second integument shows soon after the appearance of the first.

It is generally stated that ovules of Gramineae have no funiculus, but it would be impossible to draw an exact line between its presence and absence. The writer found very slight indication of a funiculus in *Agropyron repens*, merely a few slightly elongated cells at the broad region of attachment. This placental region appears to be not quite so broad here as in the case of wheat and some other grasses. The ovule attains a form which might be described as half-anatropous (fig. 20), except that the raphe characteristically present in such a type appears to be undeveloped here.[1]

The archesporium, which first became evident by its larger size and deeper stain, is in this case a single cell. There is no record of an archesporium of more than one cell among monocotyledons, with one or two exceptions reported by Coulter and Chamberlain (1903). *Agropyron repens* is typical in this respect. The development of the archesporium differs from that of the microsporangium in that there is no parietal tissue developed, nor does the primary sporogenous cell divide to form a number of sporogenous cells, so that the archesporial cell is the spore-mother-cell. In *Agropyron repens* this archesporial cell increases in size so that it becomes very prominent (fig. 15). This divides twice by periclinal walls, forming a row of four megaspores (fig. 16). The first division is the reduction division. Three of the megaspores nearest the micropyle degenerate and the one farthest away enlarges to become the embryo sac (fig. 17). One slide showed the megaspore nearest the micropyle in telophase, while the other three showed indications of mitosis. There was not enough evi dence to show whether this was merely an abnormal cell or not. The nucleus in the embryo sac divides three times in rapid succession, forming an eight-nucleate sac (figs. 18, 19, 20).

[1] The ovule in *Avena*, *Triticum*, and *Zea* is characterized by True (1893) as campylotropous, and similarly that of *Poa* is designated simply as campylotropous by Miss Andersen (1927); while Hackel (in Engler and Prantl) and Rendle (in his *Classification of Flowering Plants*) describe the ovule for grasses in general as slightly campylotropous. On the other hand, Percival calls the ovule of *Triticum* anatropous, and VanTieghem also speaks of it as anatropous or half-anatropous for the family. The published illustrations are somewhat at variance with either of these types, and indicate that the grass ovule is of a rather anomalous character, which should not be forced into any of the conventional categories.

When eight nuclei have been formed, one from each end moves toward the center of the sac and walls are laid down around the nuclei remaining at each end. The two polar nuclei do not fuse before fertilization, but they remain close together and approach the egg cell at that time. The three antipodal cells divide to form antipodal tissue, ranging from ten to sixteen cells (fig. 21). These cells are large, with distinct cell walls surrounding a darkly stained mass of cytoplasm. The nuclei take a lighter stain and contain from one to three distinct nucleoli. This is in line with the three strongly developed antipodal cells reported by Miss Andersen (1927) in *Poa pratensis* and *Poa compressa*, and the report of Weatherwax (1926) of antipodal tissue in maize, and of Cannon (1900) in *Avena*. The embryo sac at this time has enlarged, but the nucellus still remains and a definite nutritive jacket of deeply staining cells surrounds the embryo sac, which is egg-shaped with the micropylar end smaller. The larger end is filled with antipodal tissue. The question of fertilization is one of the problems which should be investigated at a later date, together with the fate of the antipodal tissue.

The fruit of *Agropyron* is a typical caryopsis, or one-celled dry indehiscent fruit with a thin membranous pericarp adhering closely to the seed, so that fruit and seed are incorporated in one body forming a single grain (True, 1893). A few experiments were tried to determine how soon after maturity seeds would germinate. Tests were made in September, as soon as the spikes were collected, in October, and in November, with no results. In January, 1927, however, fruits collected in the summers of 1925 and 1926 were found to germinate. These fruits were dissected from the spikes and put in a moist dark place, where an even temperature was maintained. Of thirty-three fruits from a spike of twenty-two spikelets collected in 1926 all but one germinated. Of seventeen fruits from a spike of eighteen spikelets collected in 1925 all but three germinated. In the spikelets dissected usually only one or two mature fruits were found, rarely three or none. In the the spikes dissected there were fruits differing from the typical light brown ones in being more slender, with greater variation as to length, and in being black. Fourteen of the black fruits ranged in length from 1.5 mm. to 5 mm. while sixty-one light brown fruits ranged from 2.5 mm. to 4 mm. None of the black

fruits germinated, so they may have contained some dominant lethal factor or some fungus growth.

The writer wishes to thank Dr. Harvey E. Stork for his helpful suggestions during the progress of this study.

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Explanation of plates 14, 15

PLATE 14. Microsporogenesis (figures ×1080 approximately).

Figs. 1–4. Formation of spireme thread, and division into chromosomes.

Fig. 5. Spindle: metaphase, first division.

Fig. 6. Telophase, first division, formation of cell plate.

Figs. 7, 8. Spindle, showing grouping of chromosomes, second division.

Fig. 9. Tetrad of microspores.

Fig. 10. Separate microspore.

Figs. 11, 12. Male gametophyte.

PLATE 15. Megasporogenesis (figs. 13-19, ×730; figs. 20, 21 ×73).

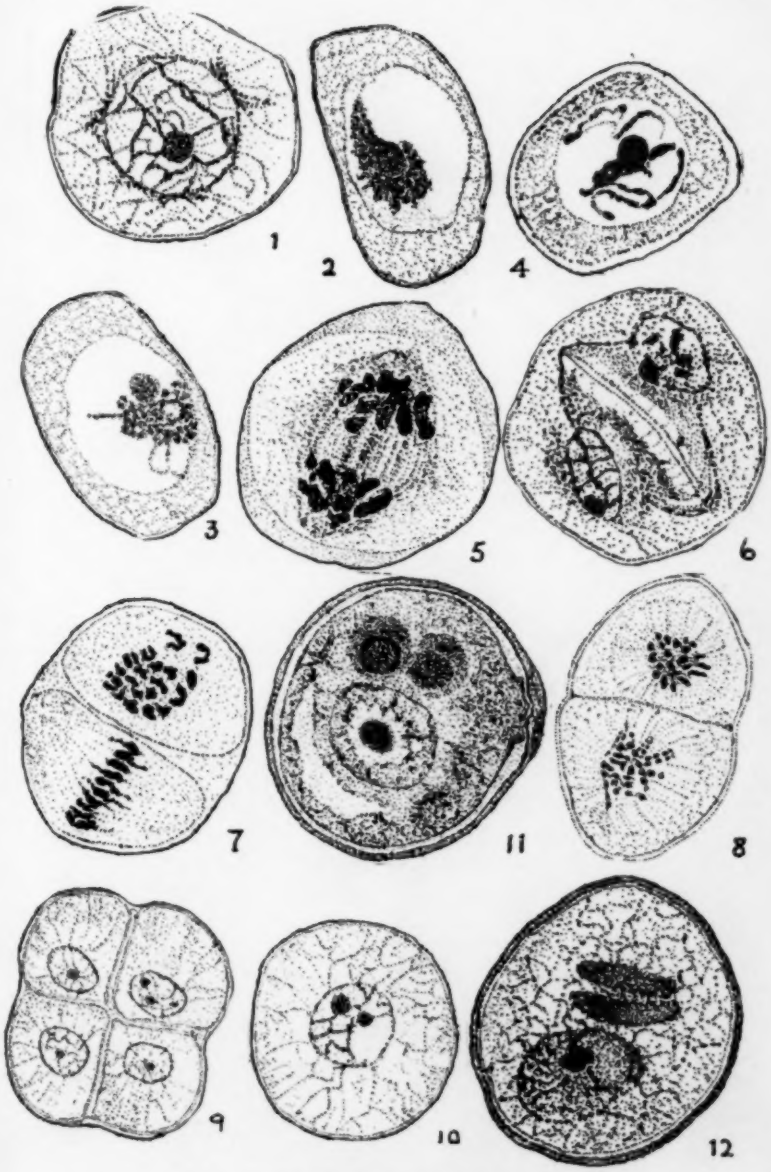
Fig. 13. Early stage in forming ovule.

Figs. 14, 15. Archesporial cell.

Figs. 16, 17. Megaspore tetrad and enlargment of functional spore.

Figs. 18–20. Embryo sac development.

Fig. 21. Female gametophyte, showing egg apparatus, antipodal tissue, and polar nuclei.



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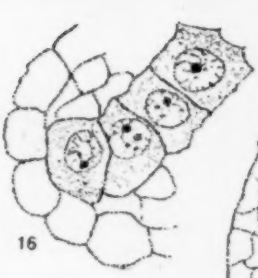
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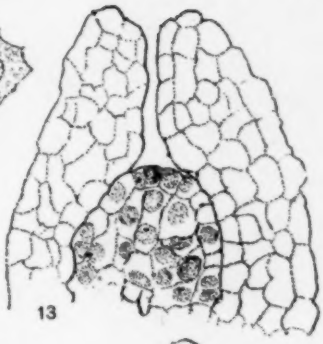
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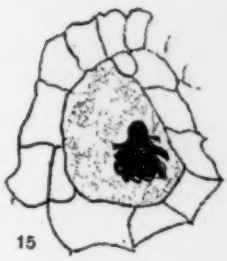
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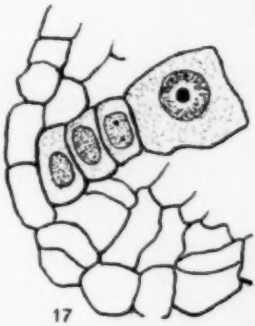
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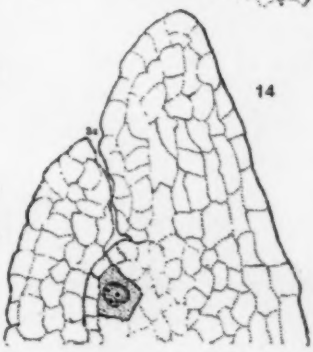
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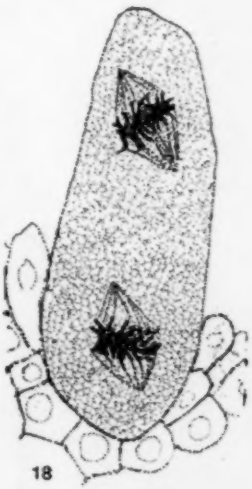
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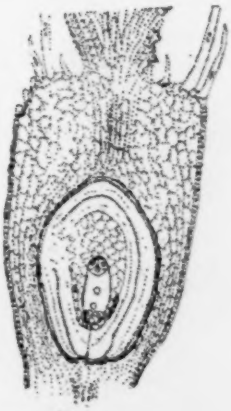
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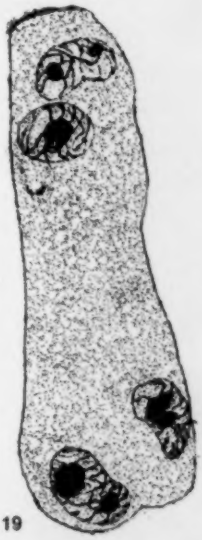
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MOWERY: AGROPYRON REPENS

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1928-1929

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